A CRITICAL EVALUATION OF AUGMENTATIVE BIOLOGICAL CONTROL

Timothy Collier[1,2] and Robert Van Steenwyk[1]
[1]Department of Environmental Science, Policy and Management
University of California, Berkeley
[2]Department of Renewable Resources,
University of Wyoming

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Correspondance:

Timothy Collier
Dept. of Renewable Resources,
University of Wyoming
Dept. 3354
1000 E. University Avenue
Laramie, WY, 82071
Office (307)766-2552
FAX: (307)766-5025
email: tcollier@uwyo.edu

Abstract

The potential for using "augmentative" biological control for suppressing arthropod pests has been recognized for many years. Nevertheless, augmentation is applied commercially in a relatively few agricultural systems. To address why this may be the case, we reviewed the augmentative biological control literature to critically evaluate three questions. First, does augmentative biological control (or "augmentation") effectively suppress agricultural pests? Second, is augmentation cost effective? Third, what ecological factors limit the effectiveness of augmentation? We evaluated effectiveness of augmentation by assessing whether pest densities were suppressed to specified target levels, and by reviewing studies that explicitly compared augmentation and conventional pesticide applications. Augmentation achieved target densities in about 15% of cases and failed more than 50% of the time. Augmentation was also often less effective than pesticide applications but not always. In the evaluation of economics, augmentative releases were frequently more expensive than pesticides, though there were cases where augmentation was clearly cost effective. Finally, 12 ecological factors were implicated as potential limits on the efficacy of augmentation. Unfavorable environmental conditions, enemy dispersal, predation on released agents, and host refuges from parasitism or predation were most often suggested as ecological limitations. We suggest that future research must identify crop-pest systems in which augmentation can cost effectively control arthropod pests using rigorous field experiments that compare augmentation with conventional pesticide applications

Introduction

The potential for using “augmentative” or “inundative” biological control to suppress arthropod pests has been recognized for many years (Doutt and Hagen 1949, DeBach 1964, Ridgway and Vinson 1977, Stinner 1977, King *et al.* 1985, Parella *et al.* 1992). Augmentative biological control (or “augmentation”) is simply the release of large numbers of insectary reared natural enemies with the goal of “augmenting” natural enemy populations or “inundating” pest populations with natural enemies. The use of augmentative releases might be appropriate, for example, if existing natural enemy populations fail to colonize fields or orchards, or colonize too late in the season to provide effective control of the pest (e.g., Obrycki *et al.* 1997).

To our knowledge, Doutt and Hagen (1949) were the first researchers to experimentally apply this approach more than 50 years ago. These authors released green lacewings to control out breaking mealybug populations in pear orchards. Since Doutt and Hagen's pioneering study, augmentative biological control has been applied experimentally in a large number of pest systems (Ridgway and Vinson 1977, Stinner 1977, King *et al.* 1985, Parella *et al.* 1992). Sales of natural enemies for augmentation have also grown considerably in recent years (Cranshaw *et al.* 1996). Nevertheless, the use of augmentation on a commercial basis appears to be limited to a few systems (van Lenteren 1988, van Lenteren *et al.* 1997).

One of the major stimuli for investigating the potential of augmentative biological control has been the drive to reduce a historic reliance on broad-spectrum pesticides for pest control. The trend in both Europe and the U.S. has been to tighten regulations on pesticide use, with some pesticides having their registrations withdrawn by governmental agencies. Augmentation might be implemented as a substitute for pesticides if the pest is sufficiently suppressed by the released natural enemies. van Lenteren (1988) argued that the first step in implementing augmentative biological control in greenhouses in the Netherlands has been to demonstrate to growers that augmentative releases are both effective and comparable in cost to pesticide applications. Here, we critically evaluate both the efficacy and cost of augmentation as an alternative to broad-spectrum pesticides in agricultural systems. We also address the ecological factors that limit the effectiveness of augmentation. We conclude by addressing how future research might promote the implementation of augmentative biological control.

Methods

Using the AGRICOLA database, we searched the key words: "biological control" and either "augmentative," "augmentation," "inundative," "inundation" or "releases." Additional studies were identified in the literature sections of papers found in the AGRICOLA searches. Over 140 studies of augmentative biological control were identified and reviewed, though only a subset of studies was analyzed in detail.

The review focused on releases of predators and parasitoids in agricultural crops. Pathogens, horticultural crops and forestry systems were not considered. In addition, there were a number of stringent (but necessary) methodological requirements. All studies included in the review were required to use the following basic experimental design. In one set of experimental units (trees, plots, fields, etc.), natural enemies were released at one or more levels and/or frequencies. In another set of experimental units, no natural enemies were released (control plots). In some cases, both control plots and release plots were treated with one or more pesticides; however, as long as pesticide applications were the same in both types of plots, the effect of augmentation could be evaluated. Some appropriate studies included pesticide applications as a third, separate experimental treatment.

A number of studies were excluded from the review because they were judged to be lacking key information or because they used an inappropriate or incomplete experimental design. Studies were excluded if they did not include experimental control plots or if control plots were clearly and/or systematically different from the treatment plots independent of natural enemy releases. Second, studies that were unreplicated were not considered further. Third, studies were excluded if they reported only percent parasitism or percent mortality as the sole measure of efficacy. Appropriate studies had to include a direct measure of pest suppression, either reduced pest densities or damage. Finally, laboratory and cage studies were excluded from consideration. Arguably, laboratory studies are unrealistic, and cage-experiments restrict the dispersal of both pests and released natural enemies. Dispersal is likely to be an important factor determining the efficacy of augmentation in the field (see below).

Efficacy of augmentation

Identifying a reasonable and widely comparable measure of efficacy was a difficult problem. In many studies, effectiveness was equated with statistically significant differences between control and release plots. Unfortunately, a number of studies misused statistics by “pseudoreplicating”, i.e., inappropriately using sampling units (leaves or plants) as experimental and statistical replicates instead of the truly independent experimental units (plots) (Hurlbert 1984). Because of pseudoreplication and because statistical significance is not necessarily equivalent to biological significance (e.g., Krebs 1999), statistical significant differences were not used as a criterion for evaluating efficacy.

Another frequent measure of effectiveness was simply the degree of suppression of pest numbers or damage in control plots versus release plots. Although this would seem to be a reasonable measure of efficacy, percent suppression alone provides incomplete information at best. A large percent suppression of a pest population achieved through augmentative releases might still be accompanied by damagingly high pest densities and excessive economic loss.

In the end, we adopted two approaches for evaluating efficacy. The first approach was based on whether the authors indicated that pest populations or damage were suppressed below some specified target density or damage level in release treatments but not in control treatments. In some cases, the specified target densities or damage levels consisted of action thresholds for pesticide application, known economically damaging levels or post-harvest standards for pest presence or damage. In other cases, authors simply stated that pest densities or damage were above or below economic targets without stating the quantitative value of the target density. Our evaluation of efficacy is thus similar to an approach taken by Stiling (1993), who evaluated the efficacy of classical biological control based on authors' assessments.

Whether or not target densities were achieved was noted for each study that provided the appropriate information. There were situations in which both control and release plots were below the threshold. In these cases, effectiveness of augmentation could not be judged (e.g., Hagley 1989, Poprawski *et al.* 1997, Lester *et al.* 1999, Michaud 2001). Finally, in studies in which multiple species of natural enemy were evaluated in separate experimental treatments, each natural enemy-pest species combination was counted as a separate case.

Our second approach for evaluating efficacy applied only to a subset of studies that explicitly compared the efficacy of augmentative releases to conventional pesticide treatments. In each of these cases, the degree of pest suppression through augmentation could be directly compared to suppression using one or more pesticide applications. Some of these studies also indicated whether pest densities were suppressed below the target level.

Implicit in our analysis is the fact that the benefits of augmentation are represented only by whether suppression was sufficient or not, or how pest control through augmentation compared to control using pesticides. Other benefits of augmentation were not considered. These difficult-to-quantify benefits include: reduced environmental impacts, improved worker safety, and prevention or postponement of pesticide resistance (van Lenteren 1988). Our method of assessing efficacy represents a novel and perhaps conservative evaluation of augmentative biological control.

Economics of augmentation

Whether or not augmentation can cost-effectively suppress pest populations has been debated since the first case studies (Flanders 1951, DeBach 1964, Stinner 1977, King *et al.* 1985, Parella *et al.* 1992). We first addressed the economic costs of augmentation by reviewing the subset of studies that explicitly presented information about economic costs, either in the form of relatively sophisticated cost-benefit analyses or simply the estimated costs of augmentation versus conventional pesticide applications. For the vast majority of remaining studies, information needed for similar analyses or comparisons were unavailable. Data on the use and costs of pesticides was problematic to obtain because a number of different pesticides are typically used to control an entire suite of pests on a given crop. It was therefore difficult to determine *a posteriori* the cost of pesticide applications as a conventional alternative to augmentation.

For many of the studies reviewed, we therefore adopted a simple approach for evaluating economics based on easily obtained information: (a) production costs for a given crop, and (b) current costs of commercially available natural enemies. For augmentation to be cost-effective, costs of releases should be small relative to overall crop production costs.

Estimated costs of production include cultivation, pest management and harvest. Values for the relevant commodities were obtained for the appropriate or closest state from the U.S.D.A. Crop Profiles Webpage (http://pestdata.ncsu.edu/cropprofiles/) in October 2003. Purchase prices for the commercially available natural enemies were obtained online in October 2003 from Rincoln-Vitova Insectaries, CA (www.rincoln-vitova.com). These values represent the *current* costs of augmentative releases for studies that may have been conducted as many as 31 years previously (Table 1).

Estimating costs of *Trichogramma* releases required a couple of assumptions. Because prices were not available for all the *Trichogramma* species used in the studies, we assumed that the *Trichogramma* species used in the studies cost the same as the species offered by Rincon-Vitova. Second, studies of augmentation using *Trichogramma* typically presented information on the number of female parasitoids released rather than number of parasitized eggs, which is the unit of sale for *Trichogramma*. We therefore assumed that on average, 0.5 female *Trichogramma* successfully emerged from each parasitized host egg, based on the results of Losey *et al.* (1995).

Additional assumptions were required to convert costs of augmentation per plant or per tree to costs per unit area, specifically for studies of augmentation in apples, corn, and hops. Some plant- or tree-density estimates were obtained from the U.S.D.A. Crop Profiles Webpage for the state in which the study was conducted or the nearest state for which data were available. Tree densities for apples (670 trees/ha) were taken from Hagley (1989).

The estimated costs of augmentation do not include all of the potential costs associated with augmentation. Because of a lack of information, the cost of augmentation does not include application costs or the costs of "scouting" or sampling pests prior to releases. Stevens *et al.* (2000) suggested that scouting and application costs for control of *Bemisia* on greenhouse poinsettias represented about 5% of the total cost of augmentation. By not considering the costs of sampling and application, the true costs of augmentation in some cases may therefore be underestimated.

Ecological Limits on Augmentation

To evaluate the ecological factors that might limit the effectiveness of augmentation, we again took the approach of Stiling (1993), who tabulated explanations for the failure of classical biological control programs based on authors' views. Although often anecdotal and potentially reflecting the biases of individual researchers, this type of information can be useful. Arguably, researchers themselves may often be in the best position to evaluate their own results. Ecological limits on the efficacy of augmentative releases were tabulated and ranked from any study that satisfied our basic criteria for inclusion, i.e., replication, the presence of acceptable controls, etc. This collection of studies includes papers that did not evaluate whether augmentation achieved target pest densities.

Results

Was augmentation effective?

Pest populations were suppressed below target densities in five out of 31 or a little more than 15% of the natural enemy-pest cases (Table 2). In six cases, pest suppression was best designated as “mixed” because suppression was adequate in some situations but not others. Losey *et al.* (1995), for example, found that releases of *Trichogramma nubilale* Ertle and Davis suppressed damage by European corn borer (ECB) *Ostrinia nubilalis* Hübner sufficiently for processed corn but not for fresh market corn. In five other cases, including three involving ECB, “mixed” suppression reflected that suppression was sufficient in some fields, some years or both. Such site-to-site and/or year-to-year variation is likely to be undesirable to growers, who are often risk averse (King *et al.* 1985, Carlson 1988). Finally, pest populations were not suppressed below specified target densities in 20 of the 31 pest-enemy cases. Thus, by our “target-density” criterion, augmentation “failed” 64% of the time.

Seven studies allowed direct comparison of the efficacy of augmentation and conventional pesticide applications (Table 3), either on the basis of specified target densities or differences in percent suppression. Pesticide treatments usually achieved target pest densities, although not always. Udayagiri *et al.* (2000), for example, reported that the conventional pesticide treatment resulted in nymphal *Lygus hesperus* Knight densities in strawberries that were near but slightly above (ca. 10-20%) the economic threshold in both years of their study. Likewise, pesticidal suppression of stinkbugs in Brazilian soybeans failed to achieve economic densities (Correa Ferreira and Moscardi 1996).

Typically, augmentation was less effective than pesticide treatments. In three of four cases, pesticides achieved target pest densities where augmentation failed to achieve target densities. In the two studies where pesticides were ineffective, augmentation with *Anaphes iole* Girault achieved sub-economic densities in one year but not the other (against *Lygus*; Udayagiri *et al.* (2000)) or also failed to achieve target densities (against stinkbugs; Correa-Ferreira and Moscardi (1996)).

In an interesting case, Trumble and Morse (1993) compared the efficacy of pesticide applications and augmentation for controlling two-spotted spider mite *Tetranychus urticae* Koch in strawberries. In their study, augmentative releases of predacious mites, *Phytoselius persimili*s Athias-Henriot, did not reduce pest densities below the economic threshold (Table 2). Conventional applications of pesticides, particularly abamectin, were very effective. Nonetheless, a combination of augmentative releases and abamectin applications provided the greatest suppression overall, both in comparison to abamectin alone and predator releases alone. Trumble and Morse's study illustrates that, although augmentation may "fail" on its own, combining augmentation with one or more pesticides may provide adequate control; this requires, of course, that pesticides are not strongly detrimental to released natural enemies.

Economics of augmentation

Four studies used cost-benefit analysis to directly evaluate the cost effectiveness of augmentation relative to conventional pesticide treatments. Olson *et al.* (1996) found that releases of a parasitoid *Gryon pennsylvanicum* Ashmead to control the true bug *Anasa tristis* De Geer on pumpkins produced lower net benefit (in dollars) than applications of esfenvalerate, 18% lower in one year and 120% lower in the next. In one year of the study, a combination of augmentative releases and planting a resistant pumpkin variety produced greater net benefit than pesticide alone, but not pesticide combined with host plant resistance. In a similar analysis, Andow (1997) calculated that releases of *Trichogramma nubilale* were considerably less cost-effective than insecticide applications used to control ECB on feed and fresh-market corn. Insecticide applications produced 87% and 45% more net benefit (in dollars) than augmentation for feed and fresh market corn respectively. In seed corn, however, *Trichogramma* releases produced essentially equivalent net benefit to insecticide treatments. In a third cost-benefit analysis of augmentation, Lundgren *et al.* (2002) showed that *Trichogramma brassicae* Bezdenko releases produced considerably less net benefit (94%; measured in cabbage head production) than methomyl treatments. Finally, Trumble and Morse (1993) showed that releases of *Phytoseilus persimilis* were cost effective in controlling two-spotted spider mite in strawberries if combined with abamectin applications. These authors calculated that the predator-release treatment produced about a third of the net benefit relative to abamectin treatments (based on strawberry yields); however, the two treatments combined produced the greatest net benefit of any of the treatments.

A more common approach for evaluating the cost effectiveness of augmentation was to directly compare estimated costs of releases versus conventional pesticide applications. For example, Moreno and Luck (1992) found that releases of *Aphytis melinus* DeBach citrus were comparable if not slightly less in cost to applications of organophosphate insecticides. In other case studies, augmentation was more expensive than pesticide treatments. Wright *et al.* (2002) reported that releases of *Trichogramma ostriniae* Pang and Chen were about half the cost of pesticide treatments; however, based on current purchase prices for *Trichogramma* rather than the authors' laboratory rearing costs, releases would have been about 1.5 times the cost of insecticidal control. In two studies, augmentative releases were about 2 times the cost of pesticide applications; this was true for releases of a parasitoid, *Theocolax elegans* Westwood, to control a stored product pest, *Rhyzopertha dominica* F. (Flinn *et al.* 1996) and releases of green lacewings, *Chrysoperla carnea* Stephens to control leafhoppers in grapes (Daane *et al.* 1996). Finally Prokrym *et al.* (1992) suggested that *Trichogramma* releases were about 6 times as expensive as insecticide treatments for *Ostrinia nubilalis* in sweet corn.

Another approach for evaluating the costs of augmentation compares the costs of augmentation estimated from current minimum costs of enemies (Table 1) to the current estimated costs of production of the commodity, which can be easily obtained (Table 2). In two systems in which releases were shown to be cost effective, *Aphytis melinus* in citrus and *Phytoselius persimilis* in strawberries, augmentation costs were estimated to be less than 1% of the production costs for these crops (Table 2). In some cases, augmentation costs were less than about 10% of the production costs, and in four of 20 cases, estimated costs of augmentation exceeded total production costs for the commodity. Obviously, augmentation was not cost effective in the latter cases.

In summary, augmentative biological control was not cost effective in many cases. There were, however, cases in which the costs and/or benefits of augmentation compared favorably to conventional control. As many authors reviewing augmentation have suggested before, analysis of cost is crucial to evaluating the potential for implementing augmentative biological control (Flanders 1951, DeBach 1964, Ridgway and Vinson 1977, Stinner 1977, King *et al.* 1985, Parella *et al.* 1992). More cost-benefit types of analysis of augmentation are clearly needed.

Ecological limits on augmentation

Of the studies included in our review, one or more ecological limitations were suggested in 20 studies for a total of 12 potential limits (Table 4). The potential limitations are discussed below in rank order based on the number of times each was cited.

<u>(1) Environment Unfavorable for Enemy (4 cases)</u>. Environmental conditions at the time of release, particularly hot and/or dry conditions, may lead to high mortality of released natural enemies. This seemed to be true for predacious mites *P. persimilis* and *Amblyseius californicus* McGregor (Pickett and Gilstrap 1986, Lester *et al.* 2001), *Trichogramma nubilale* (Andow *et al.* 1995) and the ladybird beetle *Adalia bipunctata* L. (Kehrli and Wyss 2001).

(2) Enemy Dispersal (3 cases). Dispersal of natural enemies away from the release site may limit the impact of augmentative releases. Potential examples include augmentation with green lacewings (*Chrysoperla rufilabris* Burmeister) (Grasswitz and Burts 1995) and the parasitoids *Eretmocerus eremicus* Rose and Zolnerowich (Minkenberg *et al.* 1994) and *Anaphes iole* (Norton and Welter 1996). In each case, the authors thought that the released natural enemies left the experimental plots before having much of an impact on the pest.

(3) Refuge for the Pest (3 cases). A refuge for the pest can arise when a subset of the pest population is relatively invulnerable to attack by released natural enemies. In a clear example, Udayagiri *et al.* (2000) suggested that the egg parasitoid, *Anaphes iole,* could not reach *Lygus* bug eggs deposited within strawberry fruit achenes. Eggs deposited in other parts of the fruit or plant were parasitized with much higher frequency. A similar phenomenon may arise when the crop canopy is rapidly growing and pests escape predators by colonizing new growth (Strong and Croft 1995) or if predators or parasitoids cannot physically attack all pests in a "patch" (Correa-Ferreira and Moscardi 1996).

(4) Predation (3 cases). Natural enemies released for augmentation may themselves be attacked by other "intraguild" predators. Heinz *et al.* (1999) and Ehler *et al.* (1997) implicated resident hemipterans as potential intraguild predators of augmentatively released juvenile *Delphastus catalinae* Horn and *Chrysoperla carnea*. Yu and Byers (1994) found evidence of predation on *Trichogramma brassicae*-parasitized host eggs released for control of ECB.

(5) Compensatory Mortality (2 cases). Releases of natural enemies that attack the young stages of the host may sometimes provide little reduction in crop damage if there is

"compensatory mortality", i.e., directly density dependent mortality that occurs after the mortality imposed by the augmentatively released predator or parasitoid (van Hamburg and Hassell 1984). Cloutier and Bauduin (1995) suggested that compensatory larval mortality followed predator-caused egg mortality in *Leptinotarsa decemlineata* Say, preventing a sizeable impact of predator releases. Suh *et al.* (2000) similarly suggested that releases of the egg parasitoid *Trichogramma exiguum* Pinto and Platner against *Heliothis* spp. in cotton were ineffective because of compensatory larval mortality. In another study of *Trichogramma* releases, Andow *et al.* (1995) tested and rejected the hypothesis that density dependent survival limited effectiveness of *T. nubilale* releases for ECB in corn.

<u>(6) Enemy Quality (2 cases)</u>. Consistency in the quality of natural enemies used in augmentation has been a concern for many years (Stinner 1977, Parella *et al.* 1992). Winglessness and relatively small size has been occasionally noted in mass-produced *Trichogramma*, although this explanation for failure of *Trichogramma exiguum* releases in cotton was rejected by Suh *et al.* (2000). Two studies in the review implicated enemy quality. Ehler *et al.* (1997) noted that insectary reared green lacewings (*Chrysoperla carnea*) were less able to attack bean aphid (*Aphis fabae* Scopoli complex) than wild-caught lacewings, and Norton and Welter (1996) suggested that failure of *Anaphes iole* to control *Lygus* bug may have reflected poor quality of mass-reared parasitoids.

<u>(7) Mutual Interference/Cannibalism (3 cases)</u>. Mutual interference refers to a phenomenon in which the efficiency of individual natural enemies decreases as the overall density of natural enemies is increased (e.g., Hassell 1976). This may occur if predators or parasitoids show aggressive behavior, if intraspecific contact reduces the

time available to encounter and kill pests, or if intraspecific cannibalism occurs. Wen *et al.* (1994) suggested that mutual interference explained why a higher release rate of the parasitoid *Anisopteromalus calandrae* Howard was no more effective against maize weevil than a low release rate. Kehrli and Wyss (2001) suggested that cannibalism among juvenile ladybird beetles (*Adalia bipunctata*) limited the effectiveness of releases of this species.

(8) Pest-Natural Enemy Incompatibility (2 cases). Failure of augmentative releases may simply reflect that the natural enemy is not compatible with the pest in some way. Lundgren *et al.* (2002), for example, questioned whether the strain or species of *Trichogramma* they augmentatively released (*T. brassicae*) was appropriate for suppressing *Pieris rapae* L. and *Trichoplusia ni* Hübner; parasitism and pest suppression were poor following augmentative releases. In another case, released lacewings (*Chrysoperla rufilabris*) appeared to have insufficiently fed on the target pest, *Aphis pomi* De Geer, and starved (Grasswitz and Burts 1995). Ineffectiveness of *C. rufilabris* may thus have reflected a poor match between the pest and the enemy species.

(9) Pest Immigration (2 cases). Massive influx of pests into release plots may overwhelm released natural enemies' ability to control them. Minkenberg *et al.* (1996) suggested that pest immigration, coupled with natural enemy emigration, prevented *Eretmocerus eremicus* from having any impact on whiteflies in experimental cotton plots. Similarly, immigration of Colorado potato beetle adults may have limited efficacy of releases of a combination of *Podisus maculiventris* Say and *Edovum puttleri* Grissell (Tipping *et al.* 1999).

(10) Timing of Releases (2 cases). The timing of releases during the growing season may be crucial to the effectiveness of augmentation. Two studies suggested that improper timing may have prevented sufficient suppression of grape leafhoppers by *Chrysoperla carnea* (Daane *et al.* 1996) and avocado brown mite by *Stethorus picipes* Casey (McMurtry *et al.* 1969). Two studies that explicitly varied the timing of releases showed that suppression depended on release date (Trouve *et al.* 1997; Campbell and Lilley 1999)

(11) Fungicide (1 case). Application of pesticides may cause mortality of released natural enemies and thereby limit the effectiveness of augmentative releases. Lester *et al.* (2001) suggested that fungicides applied to peaches may have limited the effectiveness of *Neoseiulus* (=*Amblyseius*) *fallacis* Garman against two phytophagous mite pests.

(12) Release Method (1 case). Augmentation requires that mass-reared natural enemies be handled during release into the field. Daane *et al.* (1996) suggested that the effectiveness of augmentative releases of *Chrysoperla carnea* in vineyards was limited by mortality imposed by handling the eggs.

In summary, our review suggested that a number of different ecological mechanisms may limit the effectiveness of augmentative biological control. Clearly, some of the limitations mentioned above might be ameliorated on the basis of further research, for instance, on better release timing, release methods, enemy quality or pest-natural enemy compatibility. The remaining limits on augmentation may seem beyond human control. In one of the case studies that explored the use of *Anaphes iole* to control *Lygus* in strawberries, for example, a refuge from parasitism appeared to limit the effectiveness of augmentative releases (Udayagiri *et al.* 2000). A refuge from parasitism would be seemingly difficult to alter. Udayagiri *et al.* suggested, however, that effective control in this system might be achieved by using releases of a second natural enemy species or application of a selective pesticide in combination with *Anaphes*. Pesticides and/or complementary releases of additional enemy species might be used to counteract a number of the other potential ecological limitations on augmentation as well: compensatory mortality, intraguild predation, and adverse environmental conditions. In general, integrating augmentative releases with other pest management practices may be instrumental in overcoming ecological limitations on the effectiveness of augmentative biological control.

Conclusions

Our goal was to use a literature review to critically evaluate three questions related to augmentative biological control. Does augmentation effectively suppress agricultural arthropod pests? Is augmentation cost effective? What ecological factors limit the effectiveness of augmentation? We found that augmentative releases were usually less effective than conventional pesticide applications, achieving target pest densities in 16% of the cases and failing in 64% of the cases. Second, augmentative releases were often more expensive than overall production costs or pesticide application costs, though there were examples of cost effectiveness. Third, a number of different ecological factors may explain why augmentation is sometimes ineffective; these factors might be overcome by altering practical aspects of augmentative releases, such as the identity or number of enemy species released, the timing of releases and/or the integration of augmentation with other management practices.

It might be argued that our approach for evaluating the efficacy of augmentation was unduly conservative. It may not seem fair to judge augmentation relative to pesticide applications or to specific target pest densities, which are undoubtedly set by a standard of pesticidal control. van Lenteren (1988) argued that low pest densities are easily achieved using relatively inexpensive and highly effective pesticides; however, such low densities may be difficult to achieve through augmentative releases. Undoubtedly, augmentation would have been effective more frequently in our review if greater damage had been acceptable. There may also have been cases in which augmentation was "effective" by some measure, but that were not included in the review because target pest thresholds had not been determined and/or were difficult to determine (e.g., Schweizer *et al.* 2002).

We would argue that there are many situations in which economic thresholds are not particularly flexible. This should be true when damage levels are set by consumer preferences or the inability of crop plants to compensate for arthropod feeding (Trumble *et al.* 1993). In these cases, greater damage is unlikely to be acceptable. We also argue that studies of augmentation must incorporate some standard for judging effectiveness besides percent suppression of pest populations or pest-induced damage. Percent suppression cannot suggest whether augmentation can effectively replace pesticide applications without some standard associated with pesticide efficacy. The goal of research on augmentation ought to be to determine whether augmentative releases can lead to acceptable pest densities, or better yet, compare augmentative releases and pesticide treatments to untreated controls, as did a number of the studies we reviewed

(Trumble and Morse 1993, Andow *et al.* 1995, Correa Ferreira and Moscardi 1996, Olson *et al.* 1996, Suh *et al.* 2000, Udayagiri *et al.* 2000, Lundgren *et al.* 2002).

Clearly, there were cases where augmentation was effective both in terms of suppression relative to target densities or pesticides, and in terms of economics. Further research might lead to successes in pest-crop systems for which augmentation had previously "failed" or produced mixed effectiveness, through releases of different enemy species or combinations of enemies, or through the integration of releases with other management practices, e.g., selective, "low-risk" pesticides. We argue that research on integrated management practices is crucial to the successful implementation of augmentative biological control.

Based on our review, augmentative biological control is unlikely to become a *panacea* for all agricultural production, and is unlikely to replace broad-spectrum pesticide use in the immediate future. Yet, the standard of conventional pesticidal control represents a moving target for studies of augmentative biological control in terms of both efficacy and cost. As less expensive, "higher-risk" pesticides are withdrawn from use, the balance may tip towards augmentation. The challenge for research on augmentative biological control is, as ever, to use rigorous field experiments to identify situations in which augmentative releases *can* work at a cost that is comparable to the pesticides that are currently available.

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Table 1. Minimum purchase prices used in economic cost assessment as given by Rincon-Vitova Insectaries (www.rinconvitova.com). Price is for adults unless otherwise shown. Recording Date: October 2003.

Natural Enemy (Authority)	Cost per 1000
Anaphes iole (Girault)	$9.50
Aphidoletes aphidomyza (Rondani)	$10.00
Aphytis melinus (DeBach)	$2.05
Chrysoperla carnea (larvae) (Stephens)	$11.40
Chrysoperla rufilabris (larvae) (Burmeister)	$11.40
Harmonia axyridis (Pallas)	$200.00
Amblysieus californicus (McGregor)	$10.60
Neoseiulus (=*Amblysieus*) *fallacis* (Garman)	$9.12
Phytoseilus persimilis (Athias-Henriot)	$7.15
"*Trichogramma* spp." (adult female)	$0.216

Table 2. Summary of analysis of the efficacy and economics of augmentative biological control in published studies. Efficacy was assessed based on author evaluation of whether pest densities exceeded specified target levels. "No. Released" is the minimum release rate that was effective in cases where releases were effective. In cases that gave mixed or insufficient suppression, "No. Released" is the full range of release rates. Costs are based on Table 1. Production costs for the commodity are based on U.S. Crop Profile data; see text. "*Trich*" abbreviated *Trichogramma*.

Pest Species (Authority)	Commodity/ Country	Natural Enemy Species	No. Released	Below Threshold?	Est. Costs of Release	Crop Prod. Costs	Ref. No
Aonidiella aurantii (Maskell)	citrus / U.S.	*Aphytis melinus* (DeBach)	50,000/ha	yes	$102/ha	$24,750-98,800/ha[a]	1
Aphis pomi (DeGeer)	apples / U.S.	*Aphidoletes aphidimyza* (Rondani)	2,800/tree	no	$18,760/ha[b]	$14,330-16,300/ha[c]	2
Aphis pomi	apples / U.S.	*Chrysoperla rufilabris* (Burmeister)	1,200/tree	no	$9,166/ha[b]	$14,330-16,300/ha[c]	2
Bemisia argentifolii (Bellows and Perring)	cotton / U.S.	*Delphastus catalinae* (Horn)	3.5-5.5 /plant	no	estimate not possible	--[d]	3
Bemisia argentifolii	cotton / U.S.	*Eretmocerus eremicus* (Rose and Zolnerowich)	not given	no	estimate not possible	--[d]	4
Cydia pomonella (L.)	apples/ Canada	*Trich. platneri* (Nagarkatti)	6,000-9,000/ha[e]	no	$1.30-1.94/ha	$14,330-16,300/ha[c]	5
Dysaphis spp.[f]	apples/ Switzerland	*Adalia bipunctata* (L.)	20-100 /tree	no	estimate not possible	--[d]	6
Erythroneura[g] *spp.*	grapes/ / U.S.	*Chrysoperla carnea* (Stephens)	22,200-37,000/ha	no	$253-421/ha	$3,000-17,000/ha[a]	7
Leptinotarsa decemlineata (Say)	tomato / U.S.	*P.maculiventris /E. puttleri*[h]	not given	no	estimate not possible	--[d]	8

Table 2. (continued). Summary of analysis of the efficacy and economics of augmentative biological control

Pest Species (Authority)	Commodity/ Country	Natural Enemy Species	No. Released	Below Threshold?	Est. Costs of Release	Crop Prod. Costs	Ref. No
Lygus hesperus (Knight)	strawberries / U.S.	*Anaphes iole* (Girault)	296,000/ha	no	$2,812/ha	$61,750-74,100/ha[a]	9
Lygus hesperus	strawberries / U.S.	*Anaphes iole*	175,000-545,000/ha	mixed[i]	$1,662-5,178/ha	$61,750-74,100/ha[a]	10
Ostrinia nubialis (Hübner)	corn / U.S.	*Trich. brassicae* (Bezdenko)	300,000/ha[e]	no[j]	$64.80 /ha	$860/ha[k]	11
Ostrinia nubialis	corn / U.S.	*Trich. ostriniae* (Pang and Chen)	75,000/ha[e]	mixed[l]	$16.20 /ha	$860/ha[k]	12
Ostrinia nubialis	corn / U.S.	*Trich. nubilale* (Ertle and Davis)	511,000-3,311,000/ha[e]	mixed[m]	$110-715/ha	$860/ha[k]	13
Ostrinia nubialis	corn / U.S.	*Trich. nubilale*	22,000-30,000/ha[e]	mixed[n]	$4.75-6.48/ha	$860/ha[k]	14
Ostrinia nubialis	corn / U.S.	*Trich. nubilale*	67,000-2,113,000/ha[e]	no[j]	$14.47-456/ha	$860/ha[k]	15
various Pentatomids[o]	soybeans / Brazil	*Trissolcus basalis* (Wollaston)	15,000/ha	no	estimate not possible	--[d]	16
Phorodon humuli (Schrank)	hops / France	*Harmonia axyridis* (Pallas)	50/plant	mixed[i]	$22,000 /ha[p]	$8,650-10,370/ha[q]	17
Pieris rapae (L.) / *Trichoplusia ni* (Hübner)	cabbage / U.S.	*Trich. brassicae*	6,517,00-7,200,000/ha[r]	no	$70.38-778/ha	$1235 /ha[s]	18
Rhizopertha dominica (F.)	stored wheat / U.S.	*Theocolax elegans* (Westwood)	0.2 /kg	mixed[i]	estimate not possible	--[d]	19

Table 2. (continued). Summary of analysis of the efficacy and economics of augmentative biological control

Pest Species (Authority)	Commodity/ Country	Natural Enemy Species	No. Released	Below Threshold?	Est. Costs of Release	Crop Prod. Costs	Ref. No
Scirtothrips citri (Moulton)	citrus / U.S.	*Euseius tularensis* (Congdon)	500-2000 /tree	no	$430- 1,730/ha[t]	$24,750- 98,880/ha[a]	20
Tetranychus mcdanieli (McGregor)	apples / U.S.	*Typhlodromus occidentalis* (Nesbitt)	128 /tree	yes	estimate not possible	--[d]	21
Tetranychus urticae (Koch)	hops / U.S.	*Neoseiulus fallacis* (Garman)	not given	no	estimate not possible	--[d]	22
Tetranychus urticae	hops / U.S.	*Metaseiulus occidentalis* (Nesbitt)	not given	no	estimate not possible	--[d]	22
Tetranychus urticae	hops / U.S.	*N. fallacis/ M. occidentalis*	not given	no	estimate not possible	--[d]	22
Tetranychus urticae	hops / U.S.	*T. pyri/ A. andersoni*[u]	not given	no	estimate not possible	--[d]	22
Tetranychus urticae	hops / U.S.	*Neoseiulus fallacis*	20-120 /plant	no	$401- $2,408/ha[p]	$8,650- 10,370/ha[q]	23
Tetranychus urticae	hops / U.K.	*Phytoseilus persimilis* (Athias-Henriot)	10/plant	yes	$157/ha[p]	$8,650- 10,370/ha[q]	24
Tetranychus urticae	corn / U.S.	*Phytoseilus persimilis*	5/plant	yes	$3,710/ha[v]	$860/ha[k]	25
Tetranychus urticae	corn / U.S.	*Amblysieus californicus* (McGregor)	5/plant	yes	$2,500/ha[v]	$860/ha[k]	25
Tetranychus urticae	strawberries / U.S.	*Phytoseilus persimilis*	12,150 /ha	no[w]	$87/ha	$61,750- 74,100/ha[a]	26

Table 2. (continued). Summary of analysis of the efficacy and economics of augmentative biological control

Notes: a. production costs for California; b. assuming 670 trees/ha (after Hagley 1989); c. production costs for WA; d. estimate or comparison not possible; e. adult females; f. *Dysaphis plantaginea* (Pass.), *D. anthrisci* (Börner), *D. chaerophylli* (Börner), and *D. radicola* (Mordv.); g. *Erythroneura variabilis* (Beamer) and *E. elegantula* (Osborn); h. combination of *Podisus maculiventris* (Say) and *Edovuum puttleri* (Grissell); i. augmentation treatment below economic threshold in one year, above threshold in the next year; j. based on acceptable damage level of 5% (Wright *et al.* 2001); l. damage above acceptable levels in some fields, below in other fields; k. production costs for WI; m. augmentation less effective at higher release rates; n. augmentation treatment suppressed damage sufficiently for processed corn but not fresh market corn; o. *Nezara viridula* (L.), *Piezodorus guildiniii* (Westwood) and *Eustichus heros* (F.); p. assuming 2,200 hop plants per hectare (est. from crop profile for WA); q. production costs based on OR and WA.; r. parasitized eggs; s. production costs for NC; t. based on costs in original paper, not current costs; u. combination of *Typhlodromus pyri* (Scheuten) and *Amblyseius andersoni* (Chant); v. assuming 70,000 corn plants per hectare; est. from crop profile for KS; w. augmentation was effective in combination with pesticide but not without.

References: 1. Moreno and Luck 1992; 2. Grasswitz and Burts 1996; 3. Heinz *et al.* 1999; 4. Minkenberg *et al.* 1994; 5. Cossentine and Jensen 2000; 6. Kehrli and Wyss 2001; 7. Daane *et al.* 1996; 8. Tipping *et al.* 1999; 9. Norton and Welter 1996; 10. Udayagiri *et al.* 2000; 11. Mertz *et al.* 1995; 12. Wright *et al.* 2001; 13. Prokrym *et al.* 1992; 14. Losey *et al.* 1995; 15. Andow *et al.* 1995; 16. Correa-Ferreira and Moscardi 1996; 17. Trouve *et al.* 1997; 18. Lundgren *et al.* 2002; 19. Flinn *et al.* 1996; 20. Grafton-Cardwell and Ouyang 1995; 21. Croft and McMurtry 1972; 22. Strong and Croft 1995; 23. Strong and Croft 1996; 24. Campbell and Lilley 1999; 25. Pickett and Gilstrap 1986; 26. Trumble and Morse 1993.

Table 3. Comparison of the efficacy of augmentation and "conventional" insecticide applications in studies that explicitly included both types of control measures in field experiments. Shown is the range of pest suppression in treatment plots relative to control plots, and whether suppression in either treatment acheived specified "target" or economic threshold pest densities. "*Trich*" abbreviates *Trichogramma*.

		Augmentation			Conventional			
Pest Species	Commodity/ Country	Natural Enemy Species	% Pest Suppress.	Below Threshold?	Insect-icide	% Pest Suppress.	Below Threshold?	Ref. No
Anasa tristis DeGeer	pumpkins / U.S.	*G. pennsyl-vanicum*[a]	43-85%[b]	--[c]	esfen-valerate	85-95%[b]	--[c]	1
Heliothine spp.[d]	cotton / U.S.	*Trich. exiguum* (Pinto and Platner)	15-33%[e]	--[c]	lambda-cyhalothrin	96-100%[e]	--[c]	2
Lygus hesperus	strawberries / U.S.	*Anaphes iole* (Girault)	51-64%[f]	mixed[g]	various[h]	45-59%[f]	marg[i]	3
Ostrinia nubialis (Hübner)	corn / U.S.	*Trich. nubilale* (Ertle and Davis)	3-72%[j]	no	various[k]	63-89%[j]	yes	4
various Pentatomids[l]	soybeans / Brazil	*Trissolcus basalis* (Wollaston)	48%[m]	no[n]	endo-sulfan	35%[m]	no[n]	5
Pieris rapae (L.)/ *Trichoplusia ni/* (Hübner)	cabbage / U.S.	*Trich. brassicae* (Bezdenko)	3%[o]	no	methomyl	63%[o]	yes	6
Tetranychus urticae (Koch)	strawberries / U.S.	*Phytoseilus persimilis* (Athias-Henriot)	15-25%[p]	no[q]	abamectin[r]	45-100%[p]	yes	7

Table 3. (continued).

Notes: a. *Gryon pennsylvanicum* (Ashmead); b. density of nymphs and adults, which varied by year and cultivar; c. “target” threshold not given; d. *Heliothis virescens* (F.) and *Heliocoverpa zea* (Boddie); e. density of late instar larvae, which varied by year; f. 2nd instar nymphs, which varied by year; g. augmentation below economic threshold in one year, above threshold in the next year; h. naled, malathion or fenpropathrin; i. near or slightly above a threshold of 0.1 nymphs/plant; j. number of larvae per 100 plants, which varied by year and cultivar; k. Capture, MVP-G or Pounce; l. *Nezara viridula* (L.), *Piezodorus guildiniii* (Westwood) and *Eustichus heros* (F.); m. number of stinkbugs per square meter; n. insufficient suppression in both treatments; o. damage rating; p. % plants infested with pest mites, which varied by year; q. augmentation was effective in combination with insecticide but not without; r. best of three pesticides.

References: 1. Olson *et al.* 1996; 2. Suh *et al.* 2000; 3. Udayagiri *et al.* 2000; 4. Andow *et al.* 1995; 5. Correa Ferreira and Moscardi 1996; 6. Lundgren *et al.* 2002; 7. Trumble and Morse 1993.

Table 4. Ecological limits on augmentative biological control in published studies. Assessment of ecological limits was based on author evaluation. "*Trich*" abbreviates *Trichogramma*.

Pest Species	Commodity/ Country	Natural Enemy Species	Below Threshold?	Ecological Limit	Ref. No
Aphis fabae (Scopoli complex)	sugarbeets / U.S.	*Chrysoperla spp.*[a]	--[b]	enemy quality/ predation	1
Aphis pomi (DeGeer)	apples / U.S.	*Chrysoperla rufilabris* (Burmeister)	no	enemy dispersal	2
Aphis pomi	apples / U.S.	*Aphidoletes aphidomyza* (Rondani)	no	pest-enemy incompatibility	2
Bemisia argentifolii (Bellows and Perring)	cotton / U.S.	*Delphastus catalinae* (Horn)	no	predation	3
Bemisia argentifolii	cotton / U.S.	*Eretmocerus eremicus* (Rose and Zolnerowich)	no	enemy dispersal/ pest immigration	4
Dysaphis spp.[c]	apples / Switzerland	*Adalia bipunctata* (L.)	no	cannibalism/ unfav. env.	5
Erythroneura spp.[d]	grapes / U.S.	*Chrysoperla carnea* (Stephens)	no	timing/release method	6
Heliothine spp.[e]	cotton / U.S.	*Trich. exiguum* (Pinto and Platner)	no	compensatory mortality	7
Leptinotarsa decemlineata (Say)	tomato / U.S.	*P.maculiventris /E. puttleri*[f]	no	pest immigration	8
Leptinotarsa decemlineata	potato / Canada	*Perillus bioculatus* (F.)	--[b]	compensatory mortality	9

Table 4. (continued). Summary of analysis of the ecological limits on augmentative biological control

Pest Species	Commodity/ Country	Natural Enemy Species	Below Threshold?	Ecological Limit	Ref. No
Lygus hesperus (Knight)	strawberries / U.S.	*Anaphes iole* (Girault)	no	enemy quality/ dispersal	10
Lygus hesperus	strawberries / U.S.	*Anaphes iole*	mixed[g]	refuge for pest	11
Oligonychus punicae (Hirst)	avocados / U.S.	*Stethorus picipes* (Casey)	--[b]	timing of release	12
Ostrinia nubialis (Hübner)	corn / U.S.	*Trich. nubilale* (Ertle and Davis)	no[h]	unfavor. environment	13
Ostrinia nubialis	corn / Canada	*Trich. nubilale*	--[b]	predation	14
various Pentatomids[i]	soybeans / Brazil	*Trissolcus basalis* (Wollaston)	no	refuge for pest	15
Pieris rapae (L.) / *Trichoplusia ni* (Hübner)	cabbage / U.S.	*Trich. brassicae* (Bezdenko)	no	pest-enemy incompatibility	16
Sitophilus zeamais (Motschulsky)	stored corn / U.S.	*Anisopteromalus calandrae* (Howard)	--[b]	mutual interference	17

Table 4. (continued). Summary of analysis of the ecological limits on augmentative biological control

Pest Species	Commodity/ Country	Natural Enemy Species	Below Threshold?	Ecological Limit	Ref. No
various Tetranychids[j]	peaches / U.S.	*Neoseiulus fallacis* (Garman)	--[k]	unfavor. env./ fungicides	18
Tetranychus urticae (Koch)	Hops / U.S.	various[l]	no	refuge for pest	19
Tetranychus urticae	corn / U.S.	*P. persimilis/ A. californicus*[m]	yes	unfavor. environment	20

Notes: a. *Chrysoperla carnea* (Stephens) or *C. rufilabris* (Burmeister); b. no specified target or economic threshold density given; c. *Dysaphis plantaginea* (Pass.), *D. anthrisci* (Börner), *D. chaerophylli* (Börner), and *D. radicola* (Mordv.); d. *Erythroneura variabilis* (Beamer) and *E. elegantula* (Osborn); e. *Heliothis virescens* (F.) and *Heliocoverpa zea* (Boddie); f. combination of *Podisus maculiventris* (Say) and *Edovuum puttleri* (Grissell); g. below threshold in one year and above threshold in the next year; h. based on acceptable damage level of 5% (Wright *et al.* 2001); i. *Nezara viridula* (L.), *Piezodorus guildiniii* (Westwood) and *Eustichus heros* (F.); j. *Panonychus ulmi* (Koch) and *Tetranychus urticae* (Koch); k. control and release plots below threshold in year of release; l. *Neoseiulus fallacis* (Garman), *Metaseiulus occidentalis* (Nesbitt), *Typhlodromus pyri* (Scheuten), *Amblyseius andersoni* (Chant) or combination; m. *Phytoseilus persimilis* (Athias-Henriot) and *Amblyseius californicus* (McGregor).

References: 1. Ehler *et al.* 1997; 2. Grasswitz and Burts 1996; 3. Heinz *et al.* 1999; 4. Minkenberg *et al.* 1994; 5. Kehrli and Wyss 2001; 6. Daane *et al.* 1996; 7. Suh *et al.* 2000; 8. Tipping *et al.* 1999; 9. Cloutier and Bauduin 1995; 10. Norton and Welter 1996; 11. Udayagiri *et al.* 2000; 12. McMurtry *et al.* 1969; 13. Andow *et al.* 1995; 14. Yu and Byers 1994; 15. Correa Ferreira and Moscardi 1996; 16. Lundgren *et al.* 2002; 17. Wen and Brower 1994; 18. Lester *et al.* 1999; 19. Strong and Croft 1995; 20. Pickett and Gilstrap 1986.